

THE SOLANUM NIGRUM COMPLEX IN
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In the large genus *Solanum*, perhaps the most widespread species-group is that contained in the section *Morella*, and centering about *Solanum nigrum* L., often known as "deadly nightshade." It consists of weedy perennials or annuals, many of which have become adventive in regions far from their original habitats. In addition, practically every continent and floral region has its indigenous members of the complex. These facts, as well as the great variability of the species, combine to make the group very difficult taxonomically. Many of the more conservative botanists, such as Gray (1886, p. 227) recognize only one species in the entire complex. On the other hand Dunal (1852, pp. 28-387), in his monographic treatment of the genus has recognized no less than 53 species in this section. An even larger number has been recognized by Bitter (1912, 1913) in his several publications on the genus.

Various members of the complex have from time to time been subjected to cytogenetic analysis. Jorgenson (1928) dealt primarily with the European species, true *S. nigrum* L. and "*S. luteum*" (= *S. villosum* Lam.). He showed that these two species have different chromosome numbers, $2n = 72$ and $2n = 48$ respectively, and can be hybridized only with the greatest of difficulty. Nakamura (1937) found that the plants growing in Japan and classified as *S. nigrum* actually comprise two distinct species, the typical *S. nigrum* with 72 chromosomes and a diploid with 24 chromosomes, which he named *S. photinocarpum* Nakamura. Cytological studies by other authors (Tokunaga 1934, Ellison 1936) have confirmed the existence of several different chromosome numbers within the complex.

Our attention was called to this complex by two observations. In the first place, the senior author noticed that the small-flowered straggling perennial which passes as *S. nigrum* in California looked obviously different from the larger flowered, thin-leaved annual which he had previously recognized by that name in the eastern United States. A count of its chromosomes showed that it was a diploid, with $2n = 24$ chromosomes. In the second place, the junior author continued an exploration of the complex, only to find that two different chromosome numbers exist among the plants passing as *S. Douglasii* Dunal. Plants from the San Francisco peninsula were hexaploids with $2n = 72$ chromosomes, while those from Monterey, the type locality for the species, and

¹ Parts of this study were carried out by the junior author during the tenure of a Mary S. Muellhaupt post-doctoral scholarship, granted by the Ohio State University.

from locations throughout central and southern California were found to be diploid, with $2n = 24$.

These observations led to a cytogenetic study of the complex by the junior author, with special emphasis on the origin of the 72 chromosome form passing as *S. Douglasii*.

This paper aims to present only the taxonomic implications of the cytogenetic investigation the complete results of which will be published elsewhere. From the taxonomic point of view, perhaps the most important fact discovered is that incompatibility as well as weakness and partial sterility of F_1 hybrids are found in crosses between members of the complex having the same chromosome numbers as well as between those with different numbers. This confirms the fact previously established by other cytogeneticists studying the complex, that several distinct species are present in it. On the other hand, hybrids between forms of typical *S. Douglasii* differing in such characters as serration and pubescence of the leaves, as well as size of the flowers, were completely fertile. This indicates that many, if not most, of the species erected by Dunal and Bitter on such trivial characters as these are invalid. Furthermore, the incomplete nature of many of the sterility barriers, as well as the occasional presence of male sterility in wild individuals clearly belonging to a good species and not of hybrid origin, suggests that in this complex some of the diploid entities are species "in the making," which have developed partial but not complete isolating mechanisms separating them from their nearest relatives. This fact undoubtedly contributes considerably to the taxonomic difficulty of the group.

In addition to these cytogenetic observations, the intimate acquaintance which the junior author made with living representatives of this group at all stages of their life history enabled him to observe many diagnostic characters not previously recognized. He showed that the hexaploid passing as *S. Douglasii* could always be distinguished morphologically from the typical diploid species, even before its chromosome number was known. This hexaploid, originally believed to be an endemic of the San Francisco Bay region, was later found to be identical with the common large-flowered *Solanum* of Chile, for which the oldest valid name is *S. furcatum* Dunal. It is an introduced weed in the San Francisco area, as well as at Westport and Trinidad, California, and in a few places on the Oregon coast. Furthermore, the authors have found that the American diploids can be distinguished morphologically from the typical European *S. nigrum*, and so are considered specifically distinct from it. Finally, it was found that the form passing in California as *S. nigrum* var. *villosum* is not the European *S. villosum* Lam., but a very different species, *S. sarachoides* Sendt., native to South America.

Therefore, while the authors are far from possessing enough knowledge to enable them to revise this difficult complex as a

whole, they feel justified in placing on record their observations on the identity and relationships of the representatives of the group which they have studied. A few synonyms have been given with the descriptions of some of the species in order to indicate the opinion of the authors as to the correct disposition of these names. However, no attempt has been made to give a complete synonymy of any of them. They may be identified by the following key:

- A. Plants conspicuously and persistently villous or hirsute; ripe berries greenish, yellow, or reddish; seeds 1.8–2.2 mm. long.
 - B. Flowers 3–8 in an inflorescence; apex of pedicel and calyx strongly expanded at maturity, the latter enveloping the lower part of the berry; ripe berry greenish 1. *S. sarachoides* Sendt.
 - BB. Flowers 1–5 in an inflorescence; pedicel and calyx not or only slightly expanded at maturity; ripe berry yellow or reddish 2. *S. villosum* Lam.
- AA. Mature growth of plants sparsely pubescent or glabrous; ripe berries black; seeds 1.2–1.8 mm. long, except in the sparingly introduced *S. nigrum* L.
 - C. Larger inflorescences usually bifurcate, the peduncle deflexed at maturity; flowers relatively large (corolla lobes 6–11 mm. long); filaments unequal in length; mature berries immediately deciduous when ripe, containing 7–34 seeds; straggling perennial 3. *S. furcatum* Dunal
 - CC. Inflorescences rarely bifurcate, the peduncle remaining erect at maturity; flowers large or small; filaments nearly or quite equal in length; mature berries persisting on the plant in the ripe condition (except in *S. americanum*), containing 25–80 seeds; perennial or annual.
 - D. Flowers large; corolla lobes 6–11 mm. long measured from the base of the corolla; anthers 2.6–4.0 mm. long; style exerted about 2 mm. beyond the anthers; stigma very slightly expanded; bushy perennial 4. *S. Douglasii* Dunal
 - DD. Flowers smaller; corolla lobes 3–7 mm. long; anthers 1.2–2.6 mm. long; style barely exerted beyond the anthers, the stigma enlarged and capitate.
 - E. Annual or perennial, the leaves firm in texture; inflorescence umbelliform or nearly so; calyx lobes all distinct from each other, reflexed at maturity; surface of berry glossy; stone cell concretions absent or few, rarely more than 3 5. *S. nodiflorum* Jacq.
 - EE. Strictly annual, the leaves thin in texture; calyx lobes unequal in length, some of them partly fused, not reflexed at maturity

- F. Inflorescence mostly umbelliform; anthers 1.4–2.0 mm. long; surface of berry glossy; seeds 1.2–1.8 mm. long; stone cell concretions always present, usually 4 to 8 per berry; berries immediately deciduous when ripe 6. *S. americanum* Mill.
- FF. Inflorescence always subracemose; anthers 1.8–2.6 mm. long; surface of berry dull; seeds 1.7–2.2 mm. long; stone cell concretions absent, or very small and not more than 1–2 per berry. 7. *S. nigrum* L.

The following notes on these seven species are based upon observations of living plants studied both in the wild and in greenhouse cultures at Berkeley, and of the large series of specimens in the Herbarium of the University of California (cited as UC), the Gray Herbarium, Harvard University (GH), the Dudley Herbarium, Stanford University (DS), and the Willamette University Herbarium, Salem, Oregon (Will.). The authors are most grateful to the curators of these herbaria for the loan of these specimens.

1. *SOLANUM SARACHOIDES* Sendt. ex Mart. Fl. Bras. 10: 18. 1846. *S. gracile*, sensu Gray, Syn. Fl. N. Am. 2 (1): 228. 1878, and Small, Man. Southeastern Flora 1114, 1933, not Link.

This species, described from Brazil and native to subtropical and temperate South America, has become widely distributed in the United States. In the flowering condition it is not unlike other members of the complex, but in fruit it is entirely different from any other species found in North America. As the berry ripens its pedicel becomes much swollen near the apex and the calyx enlarges to several times its size at anthesis. The greenish berry contains large seeds, like those of *S. villosum* and *S. nigrum*, but these are fewer in number. *S. sarachoides* is diploid, $2n = 24$.

The confusion of this species with the very different *S. villosum* Mill. of Europe seems to be based only on the fact that both species have hairy stems and leaves. Their pubescence, however, is very different in character. The stem and leaves of *S. sarachoides* are green and are thinly hirsute, with spreading, slender trichomes, while the pubescence of *S. villosum* is usually denser and more or less appressed, so that the plant looks grayish to the naked eye. The floral and fruiting characteristics mentioned above and in the key are even more distinctive.

The specimens referred to this species have been carefully compared with the description and illustration of Sendtner (*loc. cit.*), as well as with the photograph of the type specimen (Villa das Minos, Uruguay, *Sellow 281*) preserved in the Gray Herbarium. This type was at Berlin. There is no doubt that the specimens from North America agree exactly with it, as well as with other

specimens from South America. *Solanum sarachoides* is a rather common weed in arable land throughout the Pacific states, and apparently was introduced at an early date. There are two specimens in the Gray Herbarium that were collected in 1877, one from between Virginia City and Carson City, Nevada (*Hooker & Gray s.n.*), and one from Multnomah County, Oregon (*Howell 333*). It has been usually identified as *S. nigrum* L. var. *villosum* Mill., or as *S. villosum*. The following specimens may be considered typical.

BRITISH COLUMBIA. Vancouver Island, *Macoun 698* (GH); Fraser River, *Condit* in 1909 (UC).

WASHINGTON. Klickitat County: near Bingen, *Suksdorf 1480* (GH, UC). Jefferson County: near Port Townsend, *Barber 158* (GH), *Otis 2343* (UC, DS).

OREGON. Portland, *Nelson 1729* (GH); Minto's Island, Salem, *Nelson 2927* (GH). Umatilla County: Milton, *Brown 39* (UC). Union County: Fry's Point, alt. 1000 m., *Sheldon 9036* (GH).

CALIFORNIA. Solano County: Vallejo, *E. L. Greene, s.n.* (GH). Mono County: Mono Lake, *Congdon* in 1894 (GH). Humboldt County: Eureka, *Tracy 3074* (UC). San Mateo County: near Moss Beach, *Wiggins 8164* (UC, DS). Los Angeles County: La Verne, *Wheeler 1130* (UC). Orange County: Santa Ana River, *Booth 1344* (UC). Amador County: Ione, *Braunton 1200* (UC).

2. SOLANUM VILLOSUM Mill. Gard. Dict. ed. 8, no. 2. 1768; Lam. Illustr. 2: 18. 1793. *S. luteum* Mill. (*op. cit.*), no. 3, 1768. *S. alatum* Moench. Meth.: 474, 1794; Small, Man. South-eastern Flora 1114, 1933.

This European species is a rather uncommon introduction in the United States. It is characterized by its usually dense, grayish-villous pubescence; rather small, ovate leaves; yellowish or reddish berries; and large seeds. It is a tetraploid, $2n = 48$. The only specimen seen from western North America is from a plant cultivated in the University of California Botanical Garden, Berkeley (*McKay* in 1930, UC). A collection from Pensacola, Florida (*Curtiss 6493* GH, UC) consists of typical material from the eastern United States.

3. SOLANUM FURCATUM Dunal, Solan. Gen. aff. Syn. 13, n. 52. 1816. *S. chenopodioides* Lam. Illustr. 2: 18. 1793, in part. *S. rancaguense* Dunal, ex DC. Prodr. 13: 150. 1852.

Perennial, mostly straggling or reclining on other plants; the stems long and slender, with internodes longer in proportion to stem diameter than in the other species found in North America; peduncles slender, becoming strongly deflexed as the berries ripen; inflorescence racemose to cymose, the common peduncle often bifurcate at the apex; flowers large, the corolla lobes 6-11 mm. long, the sinuses shallow; filaments 1.0-2.3 mm. long, unequal; style projecting well beyond the anthers, stigma dark, capitate; berries small, deciduous immediately after ripening,

mostly with 12–25 seeds and many large stone cell concretions. Chromosome number, $2n = 72$.

The fine series of specimens of this species from Chile in the Gray Herbarium all agree in the characteristics given above, although they vary considerably in leaf shape, flower size, etc. They represent collections from all parts of central Chile, and include a duplicate of the type collection (Chile, *Dombey*, as *Witheringtonia rubra*). The following specimens from North America have been seen.

OREGON. Ballast, Linnton, *Nelson 505* (GH, DS). Curry County: The Heads, Port Orford, *Peck 20389* (Will.); near Harbor, *Peck 21262* (Will.); Port Orford, *Keck and Clausen 3428* (DS); Gold Beach, *Hoyt 44* (DS). CALIFORNIA. Humboldt County: Trinidad, *Tracy 16749* (UC). Mendocino County: Noyo, *Duncan 215* (DS); Westport, *Paddock 167, 168* (UC). San Mateo County: San Pedro Point, *Brandegge* in 1908 (UC); Mussel Rock, *Paddock 19* (UC).

Solanum furcatum looks superficially like *S. Douglasii* Dunal, but is easily recognizable upon close examination by the characters given in the above key. *S. furcatum* is apparently the common species of this complex in Chile. It is apparently the Chilean plant referred to by Lamarck (loc. cit.) in his description of *S. chenopodioides*, and has been given this name by some students of the Chilean flora. Lamarck, however, had two different plants in mind when he described this species. After the original description he cites as a locality first "Ex ins. Mauritiana," then "An *S. chenopodioides* Feuillee obs. 2. t. 14." From this it seems evident that Lamarck was describing primarily the plant from Mauritius. This is even clearer from the amplified description in his *Encyclopédie Méthodique* (1797, p. 290), in which he characterizes the plant as having 3 or 4 small flowers in an inflorescence. The species which best fits this description is the pantropical weed, *S. nodiflorum* Jacq. The type locality for *S. nodiflorum* is Mauritius, and it is the only species of the section which grows both on that island and in Chile.

In genetic behavior as well as chromosome number, *S. Douglasii* and *S. furcatum* are very different. The junior author was unable to obtain hybrids between them, even though attempts were made in both directions. Seedless, parthenocarpic fruits developed when *S. furcatum* was used as the ovulate parent. However, an artificially produced autotetraploid *S. Douglasii* produced pentaploid hybrids when crossed with the hexaploid *S. furcatum*. These hybrids were vigorous and partly fertile, setting 5 to 8 seeds per berry after artificial selfing.

In North America, *S. furcatum* is certainly a recent introduction. It occurs abundantly in only three restricted localities, all near seaports, namely San Francisco and Westport-Noyo in California, and Port Orford, Oregon. In the Westport-Noyo region the junior author has collected a distinctive narrow-petaled strain

(*Paddock 168*, UC), and one having entire-margined leaves (*Paddock 167*, UC). One or both of the writers have observed *S. furcatum* at all of its known stations in North America except for Linnton, Oregon, and at all it looks and behaves like a recently introduced weed.

4. *SOLANUM DOUGLASHII* Dunal, ex DC. Prodr. 13: 48. 1852. *S. nigrum* var. *Douglasii* Gray, Bot. Calif. 1:538. 1876.

From coastal north-central California south to Baja California, eastward through Arizona, New Mexico, and northern Mexico, southeastward at higher altitudes throughout Mexico and probably Central America. This is the common native member of the section throughout the southwestern United States and Northern Mexico, and has been well described in the various floras. Its bushy, perennial habit, large leaves and flowers, and numerous, persistent, many-seeded black berries serve to distinguish it easily from any other species found in this area. It is a diploid ($2n = 24$).

In California, where *S. Douglasii* is native and *S. nodiflorum* an introduction, the two species are quite distinct from each other. Intermediate forms have been found only in one locality, at Hecker Pass northeast of Watsonville, Santa Cruz County. In Central Mexico, however, both species are native, and they are much less well defined. All specimens seen from the tropical parts of Mexico are typical *S. nodiflorum*, while those from the higher plateau, as about Mexico City, seem indistinguishable from the northern *S. Douglasii*. In certain intermediate areas, however, as at San Luis Potosí, several specimens intermediate in character have been collected. Some of these have partly or completely abortive and sterile pollen. A few, however, have normal pollen and occasional plants with abortive pollen occur among those typical both of *S. Douglasii* and *S. nodiflorum*.

This confusing situation is perhaps explained by the hybridization experiments of the junior author. He has found that *S. Douglasii* and *S. nodiflorum* can be reciprocally hybridized rather easily, but that the F_1 hybrids have from 50 to 100 per cent of abortive pollen, and consequently are only partly fertile. Nevertheless, they yield vigorous, partly fertile progeny when back crossed to either parent. On the basis of this evidence one would not expect extensive intergradation between the species unless they had been growing side by side for some time. Nevertheless, once F_1 hybrids and their derivatives became established, they would, because of their vigorous growth and perennial habit, yield a large number of back cross progeny, which would tend to obscure the initial distinctness between the species. *Solanum Douglasii* and *S. nodiflorum* may therefore be looked upon as "borderline species," which are separated by both ecological and genetic isolating mechanisms, neither of which is perfectly developed.

The northernmost station known for *S. Douglasii* is Rockport,

Mendocino County, California (*Paddock 165*, UC). It is not known between here and southwestern San Mateo County, where it is rather common. From thence southeastward it is so well known and easily recognized that citation of specimens seems unnecessary.

5. *SOLANUM NODIFLORUM* Jacq. Ic. Pl. Rar. 2: 288. 1786. *S. chenopodioides* Lam. Illustr. 2: 18. 1793, *pro parte*. *S. photinocarpum* Nakamura et Odashima, Jour. Soc. Trop. Agr. 8: 54, fig. 2. 1936; Cytologia, Fujii Jubil. Vol.: 58. 1937. *S. nigrum* vars. *Dillenii* and *nodiflorum* Gray, Syn. Fl. North America 2 (1): 288. 1878. *S. nigrum*, sensu Jepson, Man. Fl. Plants Calif. 892. 1925, not L.

Straggling perennial; stems rounded or angled; leaves entire or sinuate-dentate; inflorescences umbelliform; calyx lobes small, thick and reflexed at maturity; flowers small; filaments and anthers variable in length, the latter 1.5–2.4 mm. long; berry shiny black, many-seeded, usually without stone cell concretions, or with 1 to 4 small ones. Chromosome number, $2n = 24$.

This and *S. nigrum*, are the two commonest, most widespread and most variable species of the section *Morella*. It apparently is an ubiquitous weed in the tropics of both hemispheres, although probably native only to the New World. The type locality is the island of Mauritius. In the western United States it is clearly introduced, probably from Mexico. It is common throughout coastal California, having been described in all of the floras as *S. nigrum*. It extends northward into Washington. Its occurrence in southern Japan and Formosa has been discussed by Nakamura (loc. cit.) who described it as a new species, *S. photinocarpum*. From seeds kindly sent by Dr. Nakamura, we have grown plants which are morphologically very similar to those collected in Berkeley. Hybrids between these two forms had better than 50 per cent fertility of pollen and seed.

The typical form of *S. nodiflorum*, with entire leaves, rounded stems, narrow corolla lobes, and short filaments, is the most common one in the tropics. In sub-tropical or warm-temperate regions the more common type has dentate leaves, angled stems and longer filaments. In a weed of this type, however, geographical subspecies or varieties are very poorly defined. In California the dentate leaved form is definitely the more common, but many specimens morphologically indistinguishable from the tropical form have been collected in southern California, where they do not show any difference in habitat preference from the dentate-leaved plants, and where all sorts of intergradations and recombinations of the character differences noted above can be found. After thorough acquaintance in the field with this species in many different countries, one might be justified in recognizing geographic segregates, but at present the wisest course is to recognize that we are concerned with an extremely variable species.

Citation of specimens of this common weed seems unnecessary; nearly all of the specimens from California identified as *S. nigrum* belong to it. In Oregon and Washington there occur puzzling integrades between it and *S. americanum*, but field studies would be necessary to determine the true status of the plants occurring in this region.

6. SOLANUM AMERICANUM Mill. Gard. Dict. ed. 8, no. 5. 1768. *S. pterocaulon* Dunal, Hist. Solan.: 153. 1813. *S. Besseri* Weinm. ex Roem. et Schultes, Syst. 4: 593. 1819. *S. nigrum* sensu Gray, Syn. Fl. N. Am. 2 (1): 227. 1886, and other American authors, in large part, not L.

Similar to *S. nodiflorum*, but always annual; leaves usually larger and thinner in texture; inflorescence usually umbellate but occasionally subracemose; flowers somewhat larger than those of *S. nodiflorum*, the corolla lobes 4.5–7.0 mm. long, from the base of the corolla; calyx thin, green, its lobes short-deltoid, unequal, some of them partly united, not reflexed at maturity; anthers 1.3–2.0 mm. long, the filaments about half as long; berries black, lustrous, many-seeded, with 2–8 stone cell concretions of moderate size. Chromosome number, $2n = 24$.

Throughout the eastern United States, south to northern Florida and Texas, west to the Great Plains, and perhaps Oregon and Washington.

With his original description, Miller does not cite the locality from which his specimens came, nor does he cite any specimens. However, the Latin description is followed by the following remark: "American nightshade like the common sort, with a small purplish flower, and smaller black berries." The flowers of the eastern American plant may be either purplish or white, but the berry is usually smaller than that of European *S. nigrum*. Since Miller characterized his species as "like the common sort," one can infer that he was describing the small herbaceous annual of temperate eastern North America, which resembles the European species considerably more closely than does the larger, sub-perennial plant of the American tropics. It is on this basis that the present authors use the name *S. americanum* for the form of the eastern United States, and *S. nodiflorum* for the tropical weed which has passed as *S. americanum* or *S. nigrum* var. *americanum* in some American floras.

Although some of the specimens from Oregon and Washington identified as *S. nigrum* approach *S. americanum* in some characteristics, others are clearly *S. nodiflorum*. No material seen from west of the Rocky Mountains is unquestionably *S. americanum*.

Typical *S. americanum* from the eastern United States, as represented by both herbarium specimens and greenhouse cultures, is very different from Pacific Coast material of either *S. nodiflorum* or *S. Douglasii*. Furthermore, hybrids between it and these species are partly or wholly sterile. The *S. nodiflorum* × *Douglasii*

hybrid has already been discussed under the description of *S. Douglasii*. That between *S. americanum* and *S. nodiflorum* has been produced twice. The first series of hybrids, between a strain of *S. nodiflorum* from Berkeley and one of *S. americanum* from Madison, Wisconsin, were weak dwarfs, which were very hard to keep alive, and flowered abortively when only a few inches tall. They were completely sterile. A second hybridization, between the Berkeley *S. nodiflorum* and *S. americanum* from Ohio, produced vigorous F₁ plants which had about 30 per cent of normal appearing pollen and from 15 to 20 per cent of normal seed set on open pollination. These two species, therefore, are separated by barriers of both hybrid inviability and hybrid sterility, but the barriers in each case are only weakly developed.

One hybridization was made between *S. Douglasii* and *S. americanum*, the parents of the hybrid being from Monterey County, California, and near Columbus, Ohio, respectively. These F₁ plants were vigorous and intermediate morphologically, except that their seeds were smaller than those of either parent. They had about 10 per cent of normal appearing pollen, and set 20 to 25 per cent of the normal number of seeds when artificially selfed. The genetic barriers between the three species *S. americanum*, *S. nodiflorum*, and *S. Douglasii* all seem therefore to be of about the same degree of development. The genetic evidence, while favoring the status of these entities as "borderline" species, would not prevent their treatment as subspecies of a single species.

The fourth member of this group in the United States, which has not been studied in the living condition but which has the pollen size of a diploid, is *S. interius* Rydb. This form, which was first described from the plains of Nebraska, is in most characteristics intermediate between *S. americanum* and *S. Douglasii*. Furthermore, a study of herbarium specimens suggests that in Nebraska, Kansas, and Texas, *S. interius* grades into *S. americanum*, while in New Mexico there are many intermediates between it and *S. Douglasii*. On the other hand, the seeds of *S. interius* are characteristically larger than those of either *S. americanum* or *S. Douglasii*, while those of the artificial hybrid between the two latter species produced by the junior author are smaller than the seeds of either of its parents. The status of *S. interius* cannot be decided until typical material of it is grown with that of *S. americanum* and *S. Douglasii*, and the necessary hybridizations are made. It is apparently the predominant form of the *S. nigrum* complex in the western Great Plains area.

7. *SOLANUM NIGRUM* L. Sp. Pl. 186. 1753. *S. Dillenii* Schultes, Oestr. Fl., ed. 2, 1: 393. 1794; non *S. nigrum* var. *Dillenii* Gray, Syn. Fl. N. Am. 2 (1): 228. 1884.

Annual; stems relatively low; leaves variable in shape, but usually entire or only slightly serrate; inflorescence subracemose;

flowers medium-sized, corolla lobes 5.5–7.5 mm. long; anthers 2.1–2.6 mm. long; berries rather large, with a dull surface, many-seeded, the seeds 1.9–2.3 mm. in diameter; concretions absent. Chromosome number, $2n = 72$.

Common and widespread in Eurasia and Africa; sparingly introduced in North America, mostly along the Atlantic seaboard. The plants of this species found occasionally in the central and western states are mostly the strain released by Burbank as the "wonderberry." This has rather large fruits, but is otherwise typical of *S. nigrum*. Its berries, like those of all of our members of this section, are edible and harmless. We find them to have a rather insipid flavor.

The distinctions between true *S. nigrum* and *S. nodiflorum* have been clearly pointed out by Nakamura (1937). *S. americanum* is more easily confused with the European species, since it is also an annual, has corollas of nearly the same size, and sometimes has subracemose inflorescences. The smaller stamens, and smaller seeds are the best diagnostic characters to separate *S. americanum* from *S. nigrum*. Furthermore, the berries of *S. nigrum* completely lack the concretions of stone cells which are found to a greater or lesser degree in all plants of *S. americanum*.

Cytologically, *S. nigrum* is very different from most of the other species of the section, since it is a hexaploid with $2n = 72$ chromosomes. The junior author has found, as expected, that the extremely vigorous hybrid between *S. nigrum* and the diploid *S. americanum* has a very irregular meiosis and 86 per cent of abortive pollen. The difference in chromosome number between these two species gives rise to an additional diagnostic character by which they may be distinguished, namely a difference in the size of the pollen grains. When mounted in water and heated so that they become spherical in shape, pollen grains from herbarium specimens of *S. nigrum* measure 24–27 μ in diameter, while those of *S. americanum*, *S. nodiflorum*, and *S. Douglasii* are only 16–20 μ in diameter. The pollen of the hexaploid *S. furcatum* is as large as that of *S. nigrum*, but these two species always can be distinguished from each other with ease. Their hybrid, *S. nigrum* \times *furcatum*, has been found by the junior author to be highly sterile and to have irregular meiotic divisions, in spite of the identity of the chromosome number of the two parents. This hybrid exhibits the growth habit of *S. furcatum*. The only specimen of true *S. nigrum* seen from Pacific North America is the following: near Forestry Building, Portland, Oregon, August 31, 1927, *J. W. Thompson*

3663 (DS).

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TWO PROBLEMS IN SALIX DISTRIBUTION

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Two peculiar problems in the distribution of certain North American species of *Salix* have confronted the writer for several years. The first problem is presented by two unrelated species having an extremely extended, but fairly continuous, distribution from south to north. The second problem is concerned with two unrelated species which have a fairly extensive, but finally discontinuous, distribution from east to west. By "unrelated" is meant that the two members of each pair belong to quite widely separated sections of the genus *Salix*.

The geographical direction of distribution given above is from the region of greater abundance to that of increasing scarcity and final disappearance. It is hoped that some one may throw light on the physiological and/or ecological factors governing these peculiar plant distributions.

A. EXTREMELY EXTENSIVE SOUTH-NORTH RANGES

The two species of *Salix* with greatly extended south-north distribution are *S. lasiandra* (accompanied by its hairy-twigged variety *lancifolia*) and *S. interior* (with its narrow-leaved variety *pedicellata*). Both species range from the latitude of northern Mexico (30°-32° N.) to the Arctic Circle or beyond (67° N.), or some 2500 miles or more. In each case, the species and its variety occur together throughout almost the entire distance.

1. *Salix lasiandra* Bentham, the Pacific or western shining